February 26, 1891.

Mr. JOHN EVANS, D.C.L., LL.D., Treasurer and Vice-President, in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

The Croonian Lecture was delivered as follows:—

CROONIAN LECTURE.—"On the Mammalian Nervous System; its Functions and their Localisation determined by an Electrical Method." By FRANCIS GOTCH, Hon. M.A., Oxford, and VICTOR HORSLEY, F.R.S., B.S., &c. (From the Physiological Laboratory, Oxford.) Received February 26, 1891.

(Abstract.)

1. *Introduction.*

In the 'Proceedings of the Royal Society,' No. 273 (vol. 45, 1889, p. 18), we published a preliminary account of some of the experiments of which the results are given in detail in our full paper.

In that communication we stated that the object of our work then was to endeavour to ascertain the character of the excitatory processes occurring in nerve fibres when either directly, *i.e.*, artificially, excited, or when in that state of functional activity which is due to the passages of impulses along them from the central apparatus. The most important way in which such a method could be applied was, obviously, one which would involve the investigation of the excitatory changes occurring in the fibres of the spinal cord when the cortex cerebri is stimulated. We must at once assume that the motor side of the central nervous system is practically divisible into three elements. (1.) *Cortical centres.* (2.) *Efferent* (pyramidal tract) *fibres*, leading down through the internal capsule, corona radiata, and spinal cord. (3.) *Bulbo-spinal centres* contained in the medulla and the spinal cord, and forming the well-known nuclei of the cranial and also of the spinal motor nerves.

It had already been determined, both by direct observation and by the graphic method (1), that certain areas of the cortex were connected with definite movements of various parts of the body, and (2) that while the complete discharge of the cortical apparatus was

followed by a very definite and characteristic series of contractions of the muscles in special relation with the particular point excited, the effectual removal of the cortical central mechanism and subsequent excitation of the white fibres passing down through the internal capsule, &c., led to the production of only a portion of the effect previously obtained from the uninjured brain.

This method of observation in no wise showed what processes were actually occurring in the spinal and other nerve fibres, and although the ablation of the cortical centre to a certain degree suggested the extent to which the cortex acted, nevertheless it did not afford an exact demonstration of the same. Moreover, the data which the graphic method furnished were precluded, through their being muscular records, from determining what share, if any, the lower bulbo-spinal central nerve cells took, either in the production of the characteristic sequence of contractions or in the modification, whether in quality or in force, of the descending nerve impulses during their transit. It seemed to us that the only way to approach this subject would be to get, as it were, between the cortex and the bulbo-spinal system of centres. This would be accomplished if some means were devised of ascertaining the character of the excitatory processes occurring in the spinal fibres of the pyramidal tract when, upon excitation of the cortex, nervous impulses were discharged from cortical cells, and travelled down the cord.

The question as to the extent to which it is possible to obtain physical evidence of the actual presence in nerve fibres of excitatory processes, and thus to arrive at reliable data for the comparison of their amounts, is one which up to the present has been answered only indirectly, and that in two ways: first, by the extension of Helmholtz's classical experiment of determining the rate of transmission, and, secondly, by observing those variations in the electrical state of nerve fibres which Du Bois-Reymond discovered to be an invariable concomitant of the excitatory state. As will subsequently be shown in the historical retrospect, it is well known, through the researches of Du Bois-Reymond and others, that the fibres of the spinal cord, just as nerve fibres in the peripheral trunks, are characterised by showing, when unexcited, an electrical difference between their longitudinal surface and cross sections; and, furthermore, that when excited, a well-marked diminution of this resisting electrical state is produced in the fibres of the cord, as in those of nerve trunks. Now, since such excitatory variations in the electrical state are presumably parallel in time and amount with the presence in the nerve of the series of unknown processes, termed excitatory, which a series of stimuli evokes, it was reasonable to presume that, if the cortex were discharging a series of nerve-impulses at a certain rate down the pyramidal tract, there would be a series of parallel changes in the

electrical condition of the fibres in the cord tract, and that, with a suitable apparatus for responding to such changes, these might be both ascertained and recorded. The accomplishment of a further purpose, viz., the localisation of both paths and centres by ascertaining the excitatory electrical effects in relation with them, was one of the main objects we had in view. In carrying it out, we found it was unnecessary to employ the electrometer, and, in fact, that it was advantageous to use the galvanometer, the record of which would be more easily and more accurately noted, since its graduation admits of far higher magnification. Moreover, with this instrument it was possible, by employing a series of stimuli, of known number and duration, to obtain quantitative results of definite comparative value, as will be shown further on; and thus, to compare both the size of different central paths and the amount of nervous energy discharged along the same path from different sources.

The plan upon which the full paper is framed is, first, to give an historical retrospect of the work of authors who have opened up the study of electrical changes in the central and peripheral nervous system; second, to describe at length our mode of experimentation, with special reference to the modifications which we have introduced, then to compare roughly the results we have obtained by our present method with those which had been previously ascertained by the graphic method, and so introduce the description of the facts which we have discovered, elucidating the physiology of the spinal cord, both in its relation to the higher centres and to the peripheral nerves.

2. *Experimental Procedure.*

The observations were in all cases made on etherised animals (cat and monkey), with due regard to the special influence of the anæsthetic. The operative procedure was so designed as to provide for suitable exposure of a particular region of the nervous system for excitation, and of another part in which the electromotive changes evoked by the stimulation may be observed. The relative parts were as follows:—

Part exposed for Excitation..	Part exposed for Observation.
Brain (cortex and corona radiata)....	and spinal cord.
Do. do. do.	and mixed nerve.
Spinal cord	and spinal cord.
Do.	and mixed nerve.
Mixed nerve	and spinal cord.
Spinal roots	do. do.
Posterior roots	and mixed nerve.

The excitation was either electrical, chemical (*i.e.*, with absinthe and strychnine), or mechanical. In the former instance the duration

and intensity were specially determined. The records were made by a Thomson high-resistance reflecting galvanometer, and a Lippmann's mercurial capillary electrometer.

The tissue, whether nerve or spinal cord, was so arranged for observation as to be always suspended in the air, one end remaining in connexion with the animal; consequently any error due to current deviations from the rest of the body could only have a slight and unipolar effect.

3. *Resting Electrical Difference between the Cut Surface of the Tissue and its Uninjured Longitudinal Surface.*

The average amounts of this difference in the tissues observed were as follows:—

	Cat.		Monkey.
Nerve	(69 cases), 0·01 Daniell	...	(12 cases), 0·005 Daniell.
Root	(5 cases), 0·025 ,,	...	—
Cord	(50 cases), 0·032 ,,	...	(9 cases), 0·022 ,,

We have observed that the cord difference is greater when that tissue is in connexion with the higher centres, and that it rises after each excitation. An important fall of the difference is to be remarked in all three tissues as a direct result of systemic death.

4. *Electrical Changes in the Spinal Cord evoked by Excitation of the Cortex Cerebri and Corona Radiata.*

We further discuss in our full paper the following points additional to those described in our previous communication, and which have resulted from the observation of the above changes:—

(*a.*) Localisation of cortical areas of representation in relation to the various regions of the cord.

(*b.*) Bilaterality of representation in the central nervous system, as evidenced by the electrical changes in the two halves of the spinal cord, consequent upon excitation of the brain or cord.

5. *Electrical Changes in the Spinal Cord when Evoked by Direct Excitation of its Fibres, after Severance from the Encephalon.*

We have by employment of this method ascertained the proportionate existence of direct channels in the various columns of the spinal cord, our design embracing the quantitative comparison of the electrical changes (and so indirectly of the nerve impulses) which are transmitted as a result of minimal excitation of the fibres. To further control our observations on these points, we have also determined the

extent of interruption in any given channel by intervening sections of the same.

As an extension of this subject, we have investigated the concurrent spread of nervous impulses to collateral paths, and probably to centres, when this further condition is introduced by increase in the stimulus.

The above results have been obtained in the case of both ascending and descending impulses.

Among other general conclusions from this division of our research are the following :—

(1.) High degree of unilaterality of representation in the spinal cord.

(2.) Spread of impulses from one posterior column to another and from one posterior column to its neighbouring lateral column through centres.

6. *The Relation of the Paths and of the Bulbo-Spinal Centres in the Spinal Cord to the Peripheral Nerves and their Roots.*

We have investigated this important relationship in the following modes :—

(I.) *The Electrical Changes in the Spinal Cord evoked by Excitation of a Mixed Nerve or its Roots.*—The chief conclusions which have been deduced from the results of these experiments, by means of minimal excitation and the employment of the method of blocking by intervening sections, include the following :—

(1.) Complete obstruction offered to centripetal impulses reaching the cord by the central end of the anterior root.

(2.) Mode of conduction, direct and indirect, in the cord of centripetal impulses passing up the posterior root.

(3.) Localisation of the direct path of afferent impulses in the posterior column of the same side as that of the nerve or root excited.

(4.) Localisation of the indirect path of afferent impulses in the posterior columns of the same and the opposite side and the lateral column of the same side as that of the nerve excited.

(5.) Proportionate development of both systems of paths in the two sides of the cord.

Expressed in percentages of the total transmission, this proportion is as follows :—

Posterior column of same side as the excited nerve...	60 p. c.
Lateral column of same side as the excited nerve.....	20 ,,
Posterior column of opposite side to the excited nerve	15 ,,
Lateral column of opposite side to the excited nerve..	5 ,,

(II.) *The Electrical Changes in a Mixed Nerve or its Roots evoked by*

Excitation of the Spinal Cord.—Whereas in the foregoing series (I) we dealt only with ascending impulses, we proceeded to investigate the distribution of descending impulses by observing the above-named changes when the individual columns of the cord are excited by minimal and later with more intense stimuli, controlling our results by the method of intervening sections.

We can summarise the effects observed as follows:—

(1.) Marked quantitative diminution suffered by impulses, leaving the spinal cord by the anterior roots, whether originating in the cortex cerebri, corona radiata, or the lateral columns of the cord.

(2.) Localisation of direct transmission of impulses in the posterior column and passing out into the posterior roots of the same side.

(3.) Proportionate development of the direct and indirect paths in the individual columns of the cord, passing out into the mixed nerve of the one side.

(4.) Effects observed in the posterior roots when the bulbo-spinal centres are excited either by strychnine or electrically (kinæsthesis).

Finally, the chief general principles elucidated by this research may be stated as follows:—

(1.) Unilateral character of the representation of function in the paths of the central nervous system.

(2.) The physiological characteristics of the regions of a nerve centre:—

(*a.*) The kinæsthetic activity of the afferent region of the centre.

(*b.*) The obstruction offered by the efferent region, including the field of conjunction, to the transmission of impulses through the centre.

Presents, February 26, 1891.

Transactions.

Baltimore:—Johns Hopkins University. Studies in Historical and Political Science. Series 9. No. 1—II. 8vo. *Baltimore* 1891.
The University.

Cracow:—Académie des Sciences. Bulletin International. Comptes Rendus des Séances. 1891. No. 1. 8vo. *Cracovie.*
The Academy.

Delft:—École Polytechnique. Annales. Tome VI. Livr. 2. 4to. *Leide* 1890.
The School.

Dublin:—Royal Irish Academy. Transactions. Vol. XXIX. Part 14. 4to. *Dublin* 1891; Proceedings. Ser. 3. Vol. I. No. 4. 8vo. *Dublin* 1891.
The Academy.